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Pollen development and degeneration in *Zebrina pendula*, with special reference to the chromosomes

ROBERT T. HANCE

(WITH PLATES 3-5)

The following work on the cultivated wandering Jew, *Zebrina pendula* Schniz., a plant which does not set seeds, was begun with the intention of studying any differences which might exist between the germinal and somatic chromosomes. So many interesting variations in the development of the pollen were found that the present paper is confined almost entirely to a description of these peculiarities.

The chief points developed in the following article are:

1. Parasynapsis occurs, which may readily be followed through the heterotypic divisions.
2. There is no fusion of chromosomes in the heterotypic division. The chromosomes appear in distinctly separated pairs. There are presumably one half as many pairs as there are somatic chromosomes and each pair behaves as a single chromosome—splitting transversely at division. Each daughter cell, therefore, receives as many *pairs* as the mother cell possessed though of one half the size.
3. The number of pairs varies from twelve to fifteen.
4. Chromosomes having the appearance, at first sight, of heterochromosomes appear, but further study shows that any chromosome may behave as such.
5. Entire chromosomes and fragments of chromosomes may be omitted from the reformed nucleus in either the heterotypic or homotypic divisions.
6. The pollen grains grow to a large size, the nucleus may or may not divide, and the cell then vacuolates and goes to pieces leaving only the outer coat shriveled and cracked.
7. Such somatic mitoses that have been observed show a long slender chromosome, whereas the germinal cells possess a short broad chromosome.

It gives me great pleasure to gratefully acknowledge the many valuable suggestions offered by Professor H. M. Benedict during the progress of my work.

MATERIAL AND METHODS

The cultivated wandering Jew was selected because of the ease with which it can be raised in the house and because it flowers steadily through the winter months.

Weak and strong Flemming's solution, equal parts of glacial acetic and absolute alcohol, and Gilson's killing agents were used and the strong solution of Flemming was found to be by far the most satisfactory. The material remained in the fixing fluid from six to twelve hours, and was washed in running water for a similar length of time.

As *Zebrina pendula* produces at various intervals from eight to twelve or more flowers at one point numerous stages may be found in a single piece of material.

Iron alum haematoxylin proved excellent but by far the best results were obtained with safranin counterstained with light green. The chromosomes are very large and when stained with safranin stand out with a sharpness that makes counting and drawing simple. The slides were allowed to remain from two and one half to three hours in safranin and from two to three seconds in light green followed by absolute alcohol, clove oil fifteen minutes, xylol three to four minutes and mounted in balsam or euparal. The latter was found to be excellent for the quickness with which it hardened and the clearness of the finished slide. Sections were cut $10\ \mu$ thick though 15 or $20\ \mu$ would be better owing to the size of the cells.

Most of the figures were drawn from the safranin preparations.

DEVELOPMENT AND DEGENERATION OF THE POLLEN

Heterotypic Division

Prophase.—The earliest stage observed is pictured in FIG. 1. The nucleus is composed of a dense network and two nucleoli stand out sharply. One is larger than the other and each is surrounded by a clear area. The growth period that ensues is figured in the next few drawings. In FIGS. 2 and 3 the cytoplasm has apparently grown away from the nucleus. This may be an

artefact, though it has been observed a number of times. In FIG. 2 the smaller nucleolus is seen to have lost a great deal of its staining capacity and is moving to the outer edge of the nucleus. It undoubtedly degenerates as only the one large nucleolus is found in succeeding stages.

As the spireme begins to form, the chromatin appears in long threads which completely fill the cavity shown in FIG. 3. The nucleolus stains less deeply but is still very distinct (FIG. 4).

FIGS. 4-7 show various steps in synapsis. FIG. 5 shows the cell developed to its maximum size. The chromatin threads of FIG. 4 have grown to form thick chromatin bands. No foundation has been found, after careful measurement of many different stages of synapsis, for the theory that synapsis is due to a growth of the cytoplasm away from the nucleus. The nucleolus is shown in FIGS. 6 and 7 (*N*). FIG. 7 shows the nucleolus beginning to vacuolate, a process which always seems to precede its disappearance.

As the chromatin bands come out of synapsis it is plainly evident that they are paired—FIG. 8. In FIG. 9, in which the paired bands are already splitting transversely to form the chromosomes, the paired nature is still more plainly visible.

Metaphase.—In the polar views of the metaphase of the pollen mother cells the chromosomes always appear in pairs. In counting great care was taken to secure uncut cells. In a few cases certain single chromosomes were counted as a pair when no other chromosome could be found near it which might be considered its mate. It was believed that its mate was probably covered by itself. With this method of counting FIG. 10 shows thirteen pairs of chromosomes, FIG. 11, thirteen pairs, FIGS. 12 and 13, twelve pairs each. FIG. 18, which, if we judge from the size of the chromosomes and their position, is the early anaphase of the heterotypic division shows fourteen pairs of chromosomes and FIG. 14, which is a similar stage, has fifteen pairs.

In FIG. 15 the two chromosomes "*X*" have all the appearances of heterochromosomes, but FIGS. 16 and 17 show that any chromosome or chromosomes may behave in a peculiar way. In FIG. 16 we find an "odd" body (*X* and *Y*) going to each pole ahead of the other chromosomes while FIG. 17 shows a pair trailing after the

others. It is safe then, I think, to conclude that no odd chromosomes occur in *Zebrina pendula* and that any chromosome may act in a manner not unlike that of the well-known accessory chromosomes.

Anaphase.—Judging from the size and position (i. e., at one end of the cell) of the chromosomes, FIGS. 14, 18, and 19 are anaphases. The paired arrangement of the chromosomes is still apparent and it is evident that the pairs are just one half the size of those in the mother cells. They have resulted from a transverse division of the chromosome pairs and in FIG. 10 the early indication of a transverse split is shown at *A* and *B*. Owing to the size of the cells it is practically impossible to find an uncut cell showing both ends of the anaphase in the same section, but FIG. 20 is a drawing carefully built up from two sections. The dark dotted line in the figure merely indicates the line of separation between the two groups of chromosomes and does not appear on the slide. 27 chromosomes appear at each pole and though the paired arrangement is not so apparent as in the preceding figures, it can still be seen in a few cases.

The dividing wall formed after the heterotypic division is pictured in FIGS. 21–23. In the first two drawings chromatic fragments are figured which trail after the other chromosomes and which probably will fail to reach the reforming nucleus in time to be included. Two entire chromosomes have been omitted from the nucleus in FIG. 23.

Homotypic Division

No dividing cells of this stage which permitted a count of the chromosomes have been found. The period of rest between the heterotypic and homotypic divisions is not very long. As in the case of the previous division, chromosomes may fail to reach the nuclei of the tetrads as shown in FIG. 25. FIG. 26 is a drawing of a complete tetrad.

The Pollen Cell

Each member of the tetrad undergoes enormous growth resulting in the pollen grains pictured in FIGS. 29 and 30. The nucleus may divide once but no later stage has ever been observed.

The cytoplasm becomes vacuolated and finally disappears entirely, leaving the cracked and shriveled outer coat, FIG. 27. Many anthers have been found filled with these empty coats.

SOMATIC MITOSIS

A single drawing of the typical somatic mitosis has been included with the others, FIG. 28. It can readily be seen that the chromosomes are strikingly different from those figured in the other drawings.

DISCUSSION

The above work is of interest in comparing the development of the pollen in normal seed producing plants with that of a plant that has lost its power of setting seeds. It is impossible to say at present whether or not the non-production of seeds is due to the irregularities appearing in the chromosome behavior. Farmer and Shove (2) consider that the varying number of chromosomes in *Tradescantia virginica* may be due "possibly to the common failure of the plant to set seeds." They, too, have recorded cases of chromatic fragments and chromosomes being omitted from the reformed nucleus and claim that they degenerate and are lost in the cytoplasm.

The question of synapsis will not be discussed here for, although I am inclined to the view of parasynapsis from the stages observed, the evidence is not sufficient as yet to base definite conclusions on. Overton (9) gives an excellent bibliography covering this question and the general field of cytology. In *Tradescantia* and *Galtonia*, Mottier (8) holds that "there is in many cells a marked tendency for some of the segments to adhere end-to-end, forming chain-like rows of sausage or kidney-shaped pieces." The peculiar conditions, however, existing in synapsis and reduction in the heterotypic divisions of *Zebrina pendula* suggest once more the question raised by Atkinson (1) as to whether, among plants, there "are not different types of chromosome reduction."

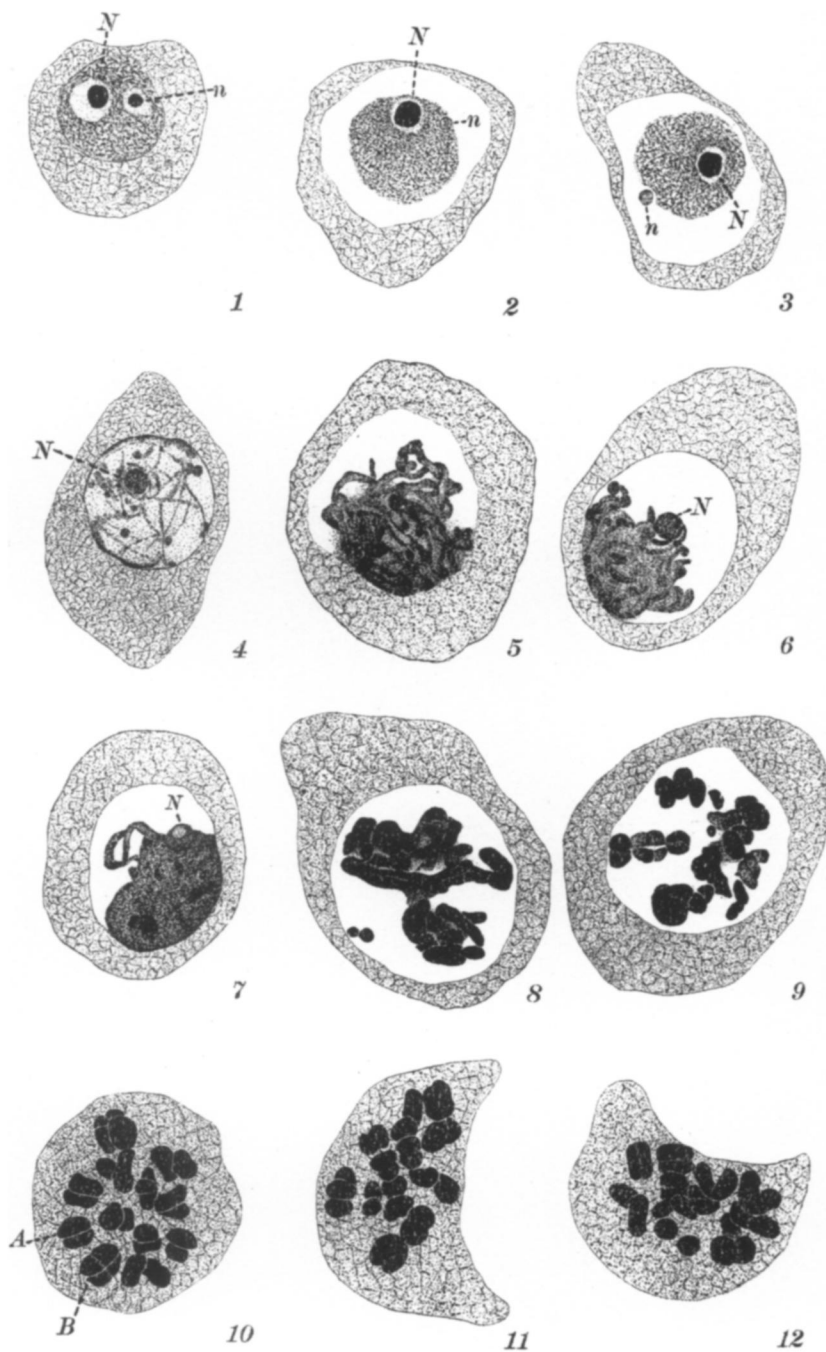
The lack of fusion between the individuals of the chromosome pairs in the heterotypic division may point to a hybrid origin. Gates (3) has cited conditions somewhat similar in hybrid *Oeno-*

theras which were sterile and has reviewed a number of other cases (4). The two germ plasms of Guyer's hybrid pigeons were found to remain separate in the cells of the testes. Speaking of a large chromosome appearing on the spindle as four small rings or vesicles, he says: "It is possible that this indicates a demarcation into tetrads, visible in hybrid material because of the firmer fusion which occurs normally at this stage is lacking. . . . It simply means, that in all probability there is an incompatibility between the chromosomes from the two different species which, in some cases, prevents them from uniting for the pseudo-reduction that normally occurs at this time." He also finds that "the division may be such that a portion of the chromatin is cut out entirely and is left behind in the cytoplasm." (5.)

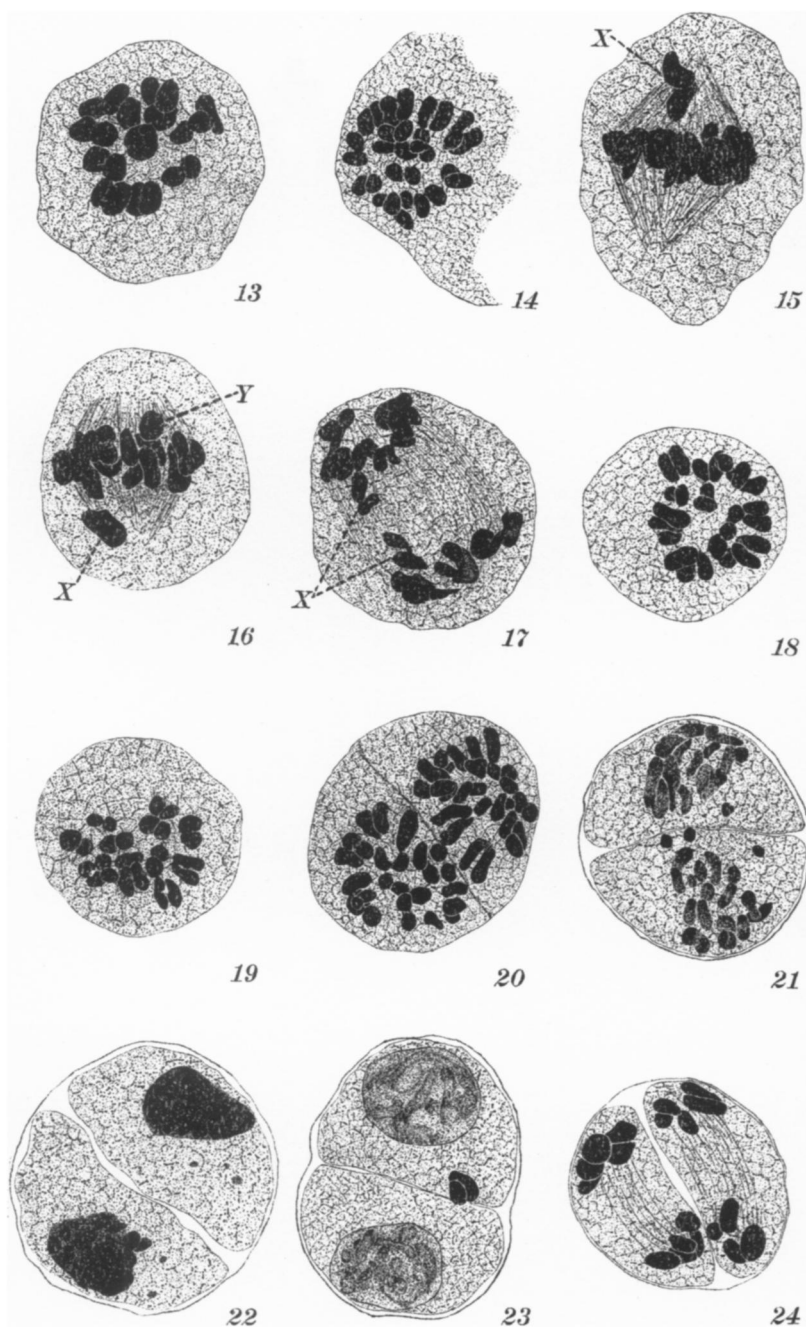
Miyaki (6) states that the reduced number of chromosomes in *T. virginica* is twelve while Farmer and Shove claim the number to vary between twelve and sixteen. In the present study the number has been found to range between twelve and fifteen.

Mottier (7) states that the chromosomes of *Tradescantia virginica* are arranged in pairs and that in the first division they may be attached end to end so that as they are drawn apart rings may be formed. Each half that goes to the poles soon appears to be paired and remains in that condition until the second division, when the members of the pair separate. This differs from the case reported in the present article in that the pairs in *Zebrina pendula* behave as single chromosomes right through the first division and no evidence of a second longitudinal division has been observed.

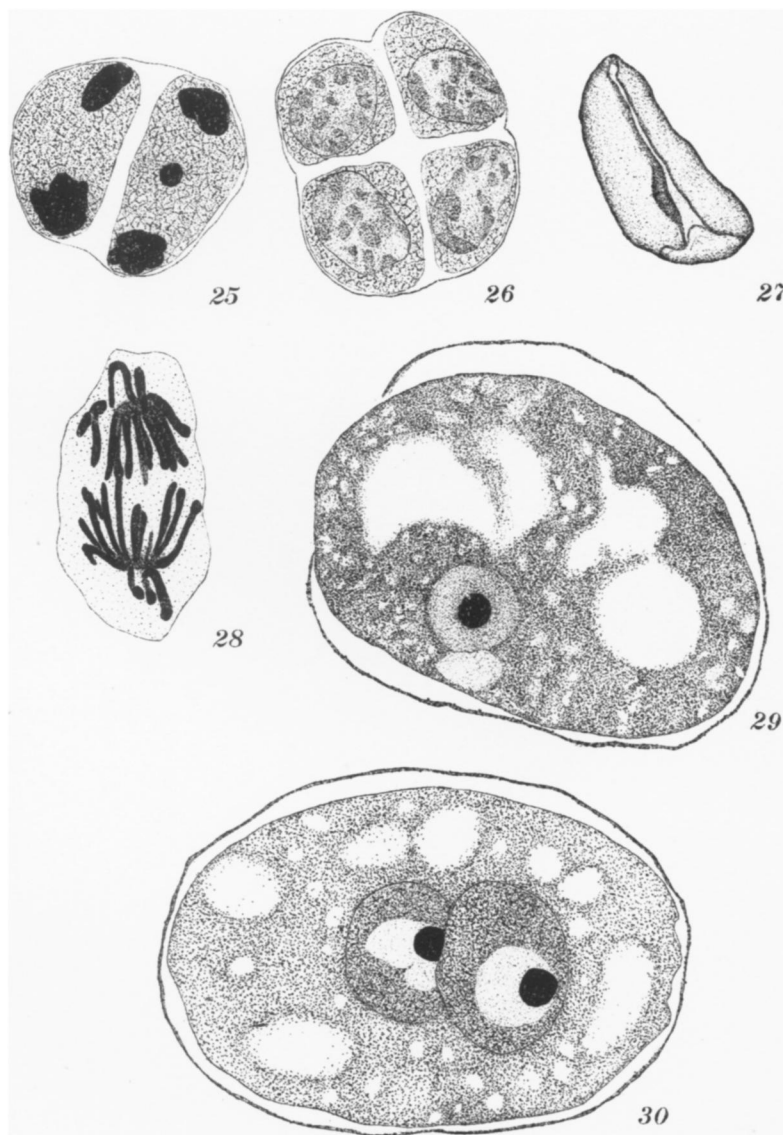
The great difference between somatic and germinal chromosomes would seem to point to the fact that chromosomes are influenced by the chemistry of the cell. The writer has observed a difference in the chromosome number of the somatic and germ cells of the pig and in another paper has discussed the importance of chromosomes in heredity from this point of view.



HANCE: POLLEN IN ZEBRINA PENDULA



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Explanation of plates 3-5

The drawings were made at table level with the aid of a Leitz camera lucida and using a Zeiss 2 mm. apochromatic objective and a No. 12 ocular. FIG. 27 is the one exception, being drawn under a 3 mm. objective and a No. 6 ocular. Drawn to the same scale as the other figures it would be about as large as FIGS. 29 and 30. The drawings are reduced one third.

SYMBOLS. *N*, large nucleolus. *X* and *Y*, "odd" chromosomes. *n*, small nucleolus. *A* and *B*, chromosomes showing preliminary split.

FIGS. 1-9. Prophase of Heterotypic Division

FIG. 1. Two nucleoli appear staining equally.

FIG. 2. Cytoplasm has grown away from nucleus. Smaller nucleolus has lost some of its staining capacity and has moved to one edge of the nucleus.

FIG. 3. Smaller nucleolus has been cast out of nucleus.

FIG. 4. Nucleus has spread to fill the cavity shown in FIG. 3. Chromatin network is beginning to form. Only one nucleolus is present.

FIG. 5. Beginning of synapsis.

FIG. 6. Later stage of synapsis showing nucleolus.

FIG. 7. Later stage of synapsis showing nucleolus beginning to vacuolate.

FIG. 8. The chromatin mass has opened up preparatory to dividing into chromosomes. The parallel arrangement of chromatin bands is apparent.

FIG. 9. Chromatin bands constricting to form the individual pairs of chromosomes. The paired arrangement is marked.

FIGS. 10-17. *Metaphase of Heterotypic Division*

- FIG. 10. Polar view showing 13 pairs of chromosomes.
 FIG. 11. Polar view showing 13 pairs of chromosomes.
 FIG. 12. Polar view showing 12 pairs of chromosomes.
 FIG. 13. Polar view showing 12 pairs of chromosomes.
 FIG. 15. Side view of spindle showing what are apparently "odd" chromosomes (X).
 FIG. 16. Same as 15 showing an odd body going to each pole (X and Y).
 FIG. 17. Early anaphase showing a pair of chromosomes trailing after the others.

FIGS. 14-23. *Anaphase of Heterotypic Division*

- FIG. 14. 15 pairs of chromosomes appear.
 FIG. 18. 14 pairs of chromosomes appear.
 FIG. 19. 13 pairs of chromosomes appear.
 FIG. 20. A drawing built up from two sections. 27 individual chromosomes can be counted as the pairing is not so obvious. The dotted line does not appear on the slide.
 FIGS. 21, 22, 23. Division completed showing reformed nuclei with chromatic fragments and whole chromosomes omitted.

FIGS. 24-26. *Homotypic Divisions*

- FIGS. 24, 25, 26. Stages in the formation of tetrad. FIG. 25 shows a chromosome omitted from the reformed nucleus.

FIGS. 27-30. *Miscellaneous*

- FIG. 27. Shows the empty and broken pollen covering.
 FIG. 28. Somatic mitosis, drawn from a dividing cell in a young sepal.
 FIG. 29. Mature pollen, a single nucleus appears and the cell is beginning to vacuolate.
 FIG. 30. Mature pollen. Two nuclei are shown.